

Diversity and decline of land snails on Rota, Mariana Islands

Scott Bauman

University of Guam, Marine Laboratory, Mangilao, Guam 96923

Abstract: This study reviews the land snail fauna of Rota to assess the diversity of the fauna (based on recent field collections and the literature) and the status of each species encountered (currently extant vs. apparently extinct but known from historically collected live specimens vs. known only from dead material). This information can be used to determine the conservation needs of land snails on Rota and to provide insights into the origin and evolutionary history of the fauna. Two known land snail predators have been introduced onto Rota since World War II: the predatory flatworm *Platydemus manokwari* De Beauchamp, 1962, and the predatory gastropod *Gonaxis kibweziensis* (Smith, 1894). Of the 43 species encountered on Rota, 9% are considered surviving well, 23% have questionable survival status, 56% are in decline, and 12% are potentially extirpated. Mariana Island land snails are more widespread among the islands of the archipelago than Hawaiian land snails. Single island endemics constitute 87% of the Oahu fauna but at most 31% of the Rota fauna. The more widespread distribution of Mariana Island land snails could be related to the frequent typhoons that track across the island group. It appears that speciation within the Mariana Islands has occurred at least in the families Assimineidae, Charopidae, and Partulidae.

Terrestrial gastropods are possibly the most extinction prone organisms on oceanic islands (Hadfield *et al.*, 1993; Paulay, 1994). Many insular land snails have restricted ranges and small population sizes, making them especially sensitive to introduced competitors, predators, and habitat destruction (Hadfield *et al.*, 1993). Also, certain species have been over-collected by shell enthusiasts in the past (Hadfield, 1986; Solem, 1990). Because many species of land snails on oceanic islands evolved *in situ*, under limited predation pressures, they tend also to possess few adaptations protecting them from introduced predators (Cowie, 1992).

Two known land snail predators have been introduced on Rota since World War II: the predatory flatworm *Platydemus manokwari* De Beauchamp, 1962, and the predatory gastropod *Gonaxis kibweziensis* (see Eldredge and Smith, 1994). The predatory gastropod *Euglandina rosea* (Férussac, 1818) has been introduced onto Guam, however, *E. rosea* was not found on Rota during 1994, 1995, or 1996. Neither is there any indication in the literature of the occurrence of this species on the island. These three predators, especially *P. manokwari* and *E. rosea*, have been implicated in declines of land snails on several Mariana Islands, as well as on other islands around the Pacific (Hadfield and Mountain, 1980; Clarke *et al.*, 1984; Murray *et al.*, 1988; Hopper and Smith, 1992).

To fully understand the evolution and biogeography of insular faunas, it is important to examine the diversity and distribution of the organisms prior to the onset of

anthropogenic activity (Balouet and Olson, 1989). The only way to do this is to sample past faunas through the fossil record. On islands the best preserved fossil faunas typically are of land snails and vertebrates. Erroneous biogeographical and evolutionary theories can be drawn from data collected only from recent faunal and floral surveys (Steadman, 1993).

In the Mariana Islands, the Partulidae have been extensively studied (Crampton, 1925; Kondo, 1970; Hopper and Smith, 1992; Smith, 1993) while other land snails have received little attention aside from taxonomic studies (Quadras and Moellendorf, 1894a, b; Baker, 1938; Abbott, 1949; Cooke and Kondo, 1961; Solem, 1983; Kurozumi, 1994). While Guam was extensively surveyed for land snails in the late nineteenth century by J. F. Quadras (Quadras and Moellendorff, 1894a, b), the other islands in the archipelago were little studied before the 1920s. Crampton and Kondo made notable land snail collections on Rota in 1925, 1949, and 1952. While numerous species have been described and recorded from Guam, few records have been published from other islands in the archipelago.

The objectives of this study were to review the land snail fauna of Rota, specifically to determine (1) the diversity of the fauna, based on recent field collections and the literature, and (2) the current status of each species (extant, apparently extinct but known from historically collected live specimens, or known only from dead material). On the basis of these data I will evaluate the conservation status of the fauna, as well as its origin and evolutionary history.

MATERIALS AND METHODS

Rota is the second southernmost island in the Mariana Islands, just north of Guam (Fig. 1). During July 1994, March 1995, and April 1996, I searched for and collected subfossil and living land snails at 26 sites on Rota (Fig. 2). Land snails other than partulids were collected at 14 of the 26 sites surveyed. The July 1994 collections were from paleontological excavations at Payapai Cave and As Matmos Cliffside Cave (sites 20 and 12 respectively). These sites along with a preliminary list of vertebrate remains from them, were described by Steadman (1992 and unpubl.). Land snails at these sites were picked from sediments sieved through *ca.* 1.6-mm mesh screens. The March 1995 survey focused on living land snails and associated land snail death assemblages (*i.e.* subfossils). This was part of a joint University of Guam and U. S. Fish and Wildlife Service survey of partulid tree snails on Rota; I was invited to survey other terrestrial snails. During April 1996, two days were spent searching for snails at two sites already studied during March 1995. At each site I searched microhabitats for live snails and also collected dead shells accu-

mulated on the forest floor. Searching less accessible microhabitats, such as under bark and deep in rock cracks, was limited at some sites because of time constraints.

Voucher specimens of all species have been deposited in the University of Guam Invertebrate Collection, and where available in sufficient numbers, in the Bernice P. Bishop Museum (BPBM). Catalog numbers cited are from the Bishop Museum's Malacological Collection catalogs.

The status of each species (Table 1) was coded as follows. A species was considered "declined" if it was collected at < 5 sites as dead shells only or if collected at > 5 sites with ≤ 20% of the sites having live animals. A species was considered "possibly extirpated" on Rota if it was collected at ≥ 5 sites with no living animals found. A species was considered to be surviving well on Rota if it was collected at > 5 sites, with ≥ 50% of the sites having living populations. Species collected at < 5 sites with some sites supporting living populations and those collected at > 5 sites with 20-50% of the sites supporting living populations were considered as surviving with uncertain status.

I have used three designations to refer to species which are not definitely identified. Species names preceded by "cf." are represented by specimens that are close to the nominal form, but differ slightly from it. Species names preceded by "aff." are represented by specimens that differ sufficiently from the nominal taxon to be considered specifically distinct. Species names preceded by a "?" refer to specimens that were either too poorly preserved for definitive identification, or whose identity with the respective nominal taxon could not be fully ascertained.

RESULTS

Tables 1 and 2 summarize the status and collection information for each species on Rota. Additional details are treated in the systematic section below.

SYSTEMATIC REVIEW

Class GASTROPODA
Subclass PROSOBRANCHIA
Family HYDROCENIDAE

Solem (1988), Thompson and Dance (1983), and Thompson and Huck (1985) provided useful recent reviews of Pacific Hydrocenidae. Three species of hydrocenids have been described from the Mariana Islands; two of these are here recorded from Rota. These are the first published records of *Georissa* from Rota.

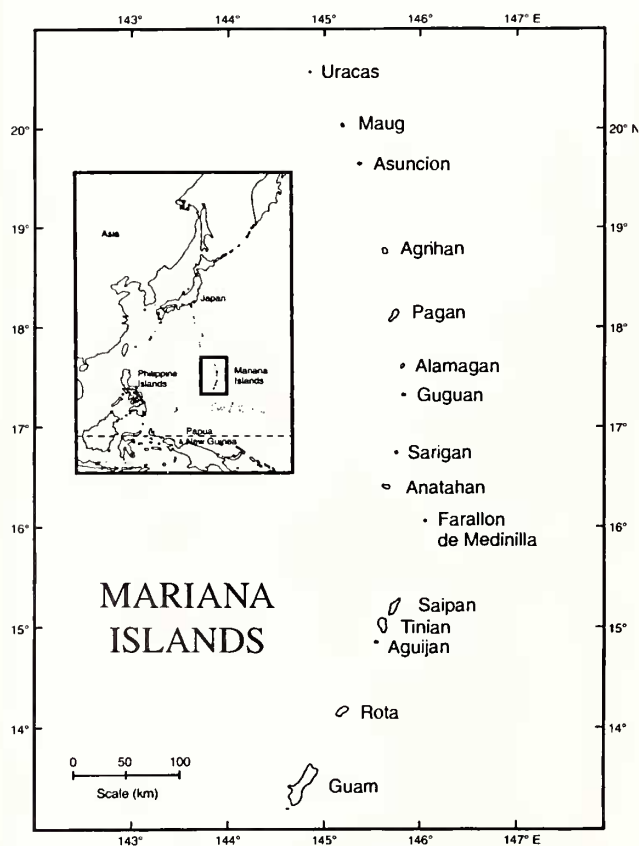


Fig. 1. Map of the Mariana Islands. Inset depicts the location of the Mariana Archipelago in the western Pacific region.

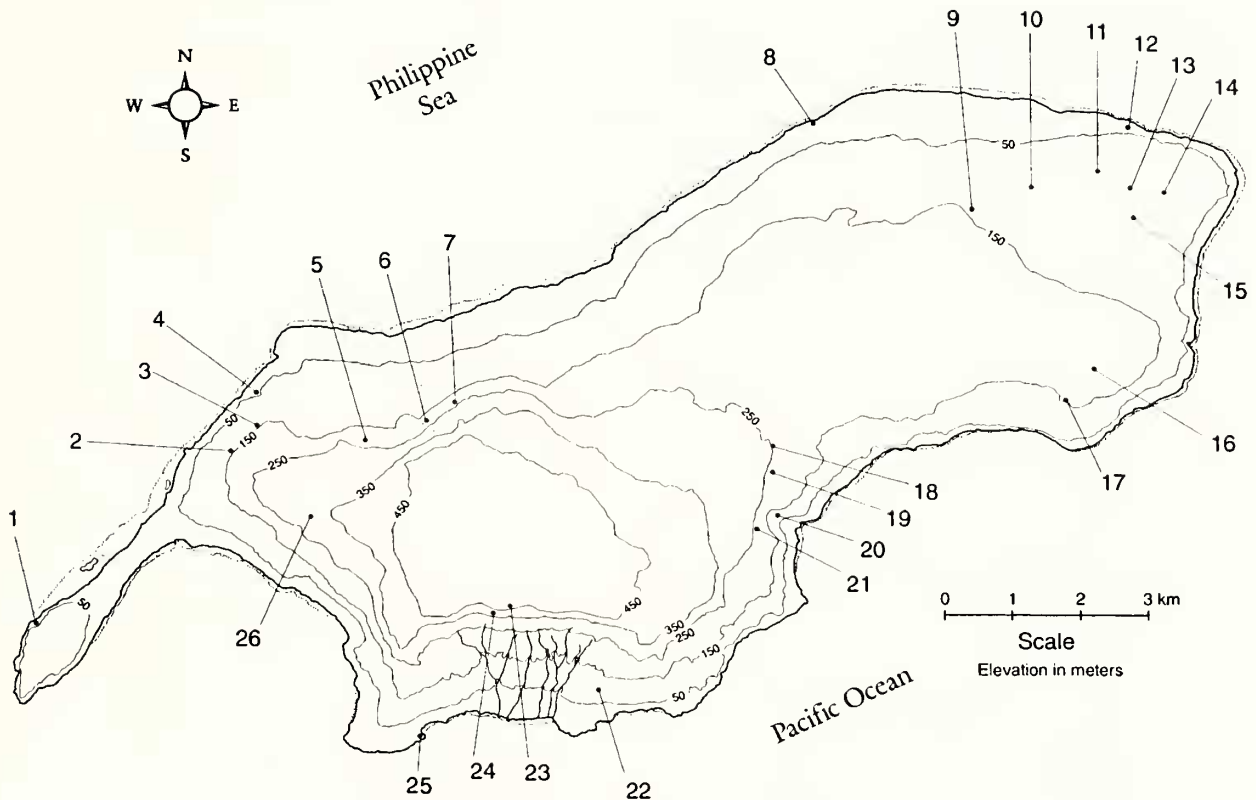


Fig. 2. Map of Rota indicating the locations of sites surveyed.

Genus *Georissa* Blanford, 1864

Georissa elegans Quadras and Moellendorff, 1894

Fig. 3

Shells of *Georissa elegans* have a sculpted and angled body whorl compared to the more rounded and weakly sculptured shell of *G. laevigata*. *G. elegans* was not found alive on Rota. *G. elegans* was described from Guam and figured by Zilch (1973a).

Georissa laevigata Quadras and Moellendorff, 1894

Fig. 4

Georissa laevigata was described from Guam and figured by Zilch (1973a). *G. laevigata* is widespread and abundant on Rota. It was found among limestone rubble and on the undersides of rotting leaves.

Family DIPLOMMATINIDAE

Genus *Palaina* Semper, 1865

Palaina taeniolata Quadras and Moellendorff, 1894

Fig. 5

This species was described from Guam; Zilch (1953) figured the lectotype. Live animals are abundant and widespread on Rota. Animals are common on the undersides of rotting leaves and on limestone rubble in forests.

Family TRUNCATELLIDAE

Fig. 6

Truncatellids tend to occur in marginal marine habitats. This habitat type was not thoroughly searched on Rota in 1995. One colony of an unidentified truncatellid was discovered on Rota in 1988 at Poña Point (B. Smith, pers. comm.). Live snails were still present at this site in 1995. No other truncatellids were found alive although numerous fragments were discovered at three other sites. Poña Point is a limestone plateau raised *ca.* 7-10 m above sea level, and is covered with short grasses growing on limestone, which has very little soil or sand and is in the spray zone of large waves. The assimineids *Omphalotropis suturalis*, and *Omphalotropis* sp. 7 are microsymbatric with this truncatellid species on Rota. The same truncatellid species and *O. suturalis* inhabit and co-occur in similar habitats on Guam.

Family ASSIMINEIDAE

The Assimineidae is the most diverse family of land snails in the Mariana Islands, with 25 species recorded from Guam (Smith, 1993). Lectotypes and holotypes of 22 species described by Quadras and Moellendorff (1894a, b) were illustrated by Zilch (1967). While only six species

Table 1. Range among the southern Mariana Islands and status of species found on Rota. Island occurrences (numbers refer to references) 1, Baker, 1938; 2, Cooke and Kondo, 1961; 3, Zilch, 1973a; 4, Zilch, 1953; 5, Zilch, 1973b; 6, Solem, 1983; 7, Kondo, 1970; 8, Abbott, 1949; 9, Smith, unpubl.; 10, Solem, 1988; 11, Tsuda, 1969; 12, Muniappan, 1983; 13, Lange, 1950; +, new record; cf., new record of cf. nominal species. Range: I, introduced; M, Mariana Islands; R, Rota endemic; W, wide ranging; +, new record; ?, range not known at this time. Status on Rota: D, declined; E, potentially extirpated; S, surviving; S?, surviving with questionable status.

Species	Island Occurrences				Range	Status on Rota
	Guam	Rota	Tinian	Saipan		
<i>Georissa elegans</i>	3	+		13	M	D
<i>G. laevigata</i>	3	+			M	S
<i>Palaina taeniolata</i>	4	+		13	M	S?
Truncatellidae sp(p).	5	+		13	?	S?
? <i>Allepithema</i> sp. 1		+			R	S?
<i>Omphalotropis cookei</i>	8	+		8	M	D
<i>O. elongatula</i>	9	+			M	E
<i>O. laevigata</i>	9	+			M	D
<i>O. octogyra</i>	9	+			M	D
<i>O. semicostulata</i>	9	+			M	D
<i>O. submariitima</i>	9	(cf.)		13	M	D
<i>O. suturalis</i>	9	+			M	S?
<i>O. quadrasi</i>	8	+			M	D
<i>O. sp. 1</i>		+			R	D
<i>O. sp. 2</i>		+			R	D
<i>O. sp. 3</i>		+			R	D
<i>O. sp. 4</i>		+			R	D
<i>O. sp. 5</i>		+			R	D
<i>O. sp. 6</i>	+	+			M	D
<i>O. sp. 7</i>		+			R	S?
<i>Paludinella conica</i>	8	+		8	M	S
<i>Quadrasiella clathrata</i>	9	+			M	D
? <i>Q. sp. 1</i>		+			R	D
<i>Pythia scarabaeus</i>	9	+		13	W	E
<i>Pacificella ?variabilis</i>	+	+			W, 1?	S?
<i>Lamellidea subcylindrica</i>	2	2			M	D
<i>L. microstoma</i>	2	2	2	2	M	
<i>Elasmias quadrasi</i>	2	2	2	2	M	S
<i>Gastrocopta</i> sp(p).	10	+		13	I,?	E
<i>Nesopupa</i> sp(p).	9	+		13	I,?	D
<i>Partula gibba</i>	7	7	7	7	M	D
<i>P. cf./aff. gibba</i>		+			R	S?
<i>Samoana fragilis</i>	7	7			M	S?
<i>Gonaxis kibweziensis</i>		11			I	D
<i>Subulina octona</i>	9	+		13	I	S?
<i>Succinea</i> sp(p).	9	+		13	?	E
<i>Achatina fulica</i>	12	12	12	12	I	E
<i>Himeroconcha</i> sp. 1		+			R	D
<i>H. sp. 2</i>		+			R	D
<i>Semperdon heptptychius</i>	6	+			M	D
<i>S. rotanus</i>	6	6			M	
<i>S. sp. 1</i>		+			R	D
<i>Liardetia tenuisculpta</i>		1		1	W	
<i>L. doliolum</i>	1	1	1		W	
<i>L. sp(p).</i>		+			?	S
<i>Lamprocystis fastigata</i>	1	1	1		M	
<i>L. sp(p).</i>		+		13	?	S?
?Genus ?species		+			I,?	D

were collected alive on Rota, an additional 13 were encountered as subfossils.

Genus *Allepithema* Tomlin, 1931

?*Allepithema* sp. 1

Fig. 7

This species is tentatively placed in *Allepithema*. It is distinct from the six species of *Allepithema* described from Guam by Quadras and Moellendorff (1894b), and is only known from Rota. A single living animal was found at each of two sites.

Genus *Omphalotropis* Pfeiffer, 1851

This is the most diverse genus of land snails on Rota and Guam. Smith (1993) listed 16 species from Guam; 15 species are here recorded from Rota.

Omphalotropis cookei Abbott, 1949

Fig. 8

Omphalotropis cookei is distinguishable from other Rota *Omphalotropis* by the presence of "pronounced spiral threads" (Abbott, 1949). Abbott (1949: 265) stated, "*O. cookei* is closest in morphological characters to *Omphalotropis erosa* (Quoy and Gaimard, 1832) from Guam," but that species was not found on Rota. *O. cookei* is closest morphologically to *O. elongatula*, on Rota.

Omphalotropis cookei was previously known from Guam and Saipan (Abbott, 1949). Although this species was found dead at seven sites, only a single living population was encountered on Rota. Live animals were collected from the undersides of decaying leaves. *O. cookei* appears to have declined on Rota.

Omphalotropis elongatula Quadras and Moellendorff, 1894

Fig. 9

Previously known only from Guam, *Omphalotropis elongatula* is closest to *O. cookei* on Rota (see above). No live animals of *O. elongatula* were found on Rota during 1994 or 1995.

Omphalotropis laevigata Quadras and Moellendorff, 1894

Fig. 10

Omphalotropis laevigata was described from Guam. Shells which nearly match figured specimens from Guam (Zilch, 1967) were found at As Matmos Cliffside Cave on Rota.

Omphalotropis octogyra Quadras and Moellendorff, 1894

Fig. 11

Previously known only from Guam, *Omphalotropis octogyra* was abundant as subfossils at one site on Rota. Many *O. octogyra* shells collected at this site appeared to be fresh (still covered with periostracum). At this site only one land snail species was found alive (*Georissa elegans*),

although 14 other land snail species were found as subfossils in leaf litter and soil samples. Traces of the predatory flatworm, *Platydemus manokwari*, were noted at this site.

Omphalotropis semicostulata Quadras and

Moellendorff, 1894

Fig. 12

This species was previously known only from Guam. No living animals were found.

Omphalotropis cf. *submaritima* Quadras and

Moellendorff, 1894

Fig. 13

Omphalotropis cf. *submaritima* can be distinguished from the similar *O. suturalis* by its larger size and more rounded sutural ramps. Dead shells of *O. cf. submaritima* were found at one site on Rota. Previously this species was only known from Guam and Saipan.

Omphalotropis suturalis Quadras and Moellendorff, 1894

Fig. 14

Omphalotropis suturalis was described from Guam and is only known from two populations on Rota. This species appears to be restricted to coastal margins of forests; both on Guam (pers. obs.) and Rota.

Omphalotropis quadrasi Moellendorff, 1894

Fig. 15

Abbott (1949) redescribed and figured *Omphalotropis quadrasi*, then considered a Guam endemic. One fresh *O. quadrasi* shell was found at one site on Rota.

Omphalotropis "carinate" species complex (species 1-5)

Seventeen specimens collected as subfossils at two locations on Rota appear to represent a previously unrecognized species complex characterized by turriculate shells ornamented by a well-developed carina. All of the species appear to be undescribed and no species like them have been collected on Guam to date. They could represent an endemic radiation of assimineids on Rota. They are tentatively included in *Omphalotropis* on the basis of Thiele's (1929: 172) definition of the genus: "Shell oval to turriculate, with perforated umbilicus, surrounded by a more or less distinct ring; aperture oval, apertural margin in most cases interrupted, occasionally somewhat broadened." At present five species are recognized, but as material to evaluate variation is limited, this number might have to be revised in the future. All five putative species possess the generic characters mentioned by Thiele except apertural characters cannot be resolved in all specimens due to their poor preservation.

Table 2. Distribution and collection status of each species found on Rota. F, subfossil collection; FL, collected both subfossil and live; L, collected alive.

SPECIES	SITE NUMBER														
	1	2	4	6	7	8	10	11	12	17	20	21	24	25	
<i>Georissa elegans</i>	F					F	F				F				
<i>G. laevigata</i>	F	FL	L	L	L	FL	F	F		FL	FL		L		
<i>Palaina taeniolata</i>	F	F	L	L		F	F	F	F	F	FL		L		
Truncatellidae						F			F		F			L	
? <i>Allepithema</i> sp. 1				L							F		L		
<i>Omphalotropis cookei</i>	F	F	L			F		F		F	F				
<i>O. elongatula</i>	F	F				F	F			F	F				
<i>O. laevigata</i>									F						
<i>O. octogyra</i>		F													
<i>O. semicostulata</i>						F					F				
<i>O. cf. submaritima</i>		F													
<i>O. suturalis</i>						FL			F		F			L	
<i>O. quadrasi</i>												F			
<i>O. sp. 1</i>									F		F				
<i>O. sp. 2</i>									F		F				
<i>O. sp. 3</i>											F				
<i>O. sp. 4</i>											F				
<i>O. sp. 5</i>											F				
<i>O. sp. 6</i>	F	F		L			F			F	F				
<i>O. sp. 7</i>														L	
<i>Paludinella conica</i>	FL	F	L	L	L	F	F		F	F	F	F	L		
<i>Quadrasiella clathrata</i>											F				
? <i>Q. sp. 1</i>											F				
<i>Pythia scarabaeus</i>	F	F				F			F	F	F	F	F		
<i>Pacificella ?variabilis</i>	FL								F		F				
<i>Lamellidea subcylindrica</i>	F	F				F			F	F	F		L		
<i>Elasmias quadrasi</i>	FL	F					F	FL	F	F	FL		L		
<i>Gastrocopta</i> sp(p).	F					F	F		F	F	F	F			
<i>Nesupupa</i> sp(p).	F										F				
<i>Partula gibba</i>	F	F	L	L	F	FL	F	F	F	F	FL		FL		
<i>P. cf./aff. gibba</i>									F		F				
<i>Samoana fragilis</i>													L		
<i>Gonitaxis kibweziensis</i>			F												
<i>Sublina octona</i>	Encountered at many sites around Rota.														
<i>Succinea</i> sp(p).	F	F						F	F		F	F	F		
<i>Achatina fulica</i>	Encountered at many sites around Rota.														
<i>Himeroconcha</i> sp. 1								F		F					
<i>H. sp. 2</i>										F					
<i>Semperdon heptapychius</i>						F				F					
<i>S. sp. 1</i>										F					
Charopid sp(p.) indet.		F		F				F							
<i>Liardetia</i> sp(p.)	FL		L			FL	F	FL		F	FL	FL	L		
<i>Lamprocystis</i> sp(p.)	FL	F		L		F	F		F	F	F		L		
?Genus ?species									F						

Omphalotropis sp. 1

Fig. 16

Shell small, globose, and with carina not reaching the apex. Known from 11 specimens from excavation at sites 12 and 20.

Omphalotropis sp. 2

Fig. 17

Shell similar to *Omphalotropis* sp. 1 but slightly larger with a higher, thinner spire. Known from one specimen each from excavations at sites 12 and 20.

Omphalotropis sp. 3

Fig. 18

Shell high spired, cyrtoconoid (with convex sides); suture channeled with a somewhat prominent carina. Site 20 yielded two specimens from excavations.

Omphalotropis sp. 4

Fig. 19

Shell slightly smaller and similar to *Omphalotropis* sp. 3, high spired, cyrtoconoid, with carina not as prominent. One specimen was collected from excavation at site 20.

Omphalotropis sp. 5

Fig. 20

Shell close to *Omphalotropis* sp. 4 but the carina is near the middle of a whorl. Known from one specimen from excavation at site 20.

Omphalotropis sp. 6

Fig. 21

Omphalotropis sp. 6 is conchologically close to *O. elongatula* and *O. cookei* on Rota and to *O. erosa* (Quoy and Gaimard, 1832) from Guam. *O.* sp. 6 was found living under limestone rubble in the forest, but not on the undersides of decaying leaves. They were moderately abundant.

Omphalotropis sp. 7

Fig. 22

This species was only found at Poña Point living sympatrically with *Omphalotropis suturalis* and a truncatellid. It is similar in shell shape to *O. suturalis* but differs by being finely ribbed. Of the three species found at Poña Point, *O.* sp. 7 is the rarest in my collections.

Genus *Paludinella* Pfeiffer, 1841*Paludinella conica* (Quodras and Moellendorff, 1894)

Fig. 23

Paludinella can be separated from the similar genus *Assimineia* Fleming, 1828, by the absence of a fine spiral thread just below the suture (Abbott, 1949). *P. conica* is the

most abundant and widespread assimineid on Rota. Living specimens occurred at five sites and were noted as common at many locations by U. S. Fish and Wildlife Officers on Rota. They were also found as subfossils at seven other sites.

Genus *Quadrasiella* Moellendorff, 1894

Quadrasiella was erected by Moellendorff in Quodras and Moellendorff (1894b) for two species of land snails on Guam; Moellendorff (1900) described a third species from Pohnpei (Caroline Islands). *Quadrasiella* is differentiated from other assimineids by its operculum, which has an "inner calcareous lamella which overlaps the peristome" (Moellendorff, 1900: 119).

Quadrasiella clathrata Moellendorff, 1894

Fig. 25

This species, previously known only from Guam, was figured by Zilch (1967). On Rota it was found in excavations at site 20.

? *Quadrasiella* sp. 1

Fig. 24

? *Quadrasiella* sp. 1 is conchologically similar to *Q. clathrata* from Guam. It differs from *Q. clathrata* in that the body whorl does not expand as fast, the spire is higher, and the sculpture is more prominent. No opercula were found in association with the new specimens, thus its generic status is uncertain. This species is known only from Rota.

Subclass PULMONATA

Order ARCHAEPULMONATA

Family ELLOBIIDAE

Genus *Pythia* Röding, 1798*Pythia scarabaeus* (Linné, 1758)

Pythia scarabaeus ranges widely on islands in the western Pacific. Shells of this species are a highly visible component of the ground shell paleofauna in many forested areas on Rota. No living animals were found. Bishop Museum records indicate that the species was common alive on Rota in 1925 and 1949 (BPBM 213232, 213261, and 82427). Subsequently *P. scarabaeus* has declined and could be extirpated on Rota.

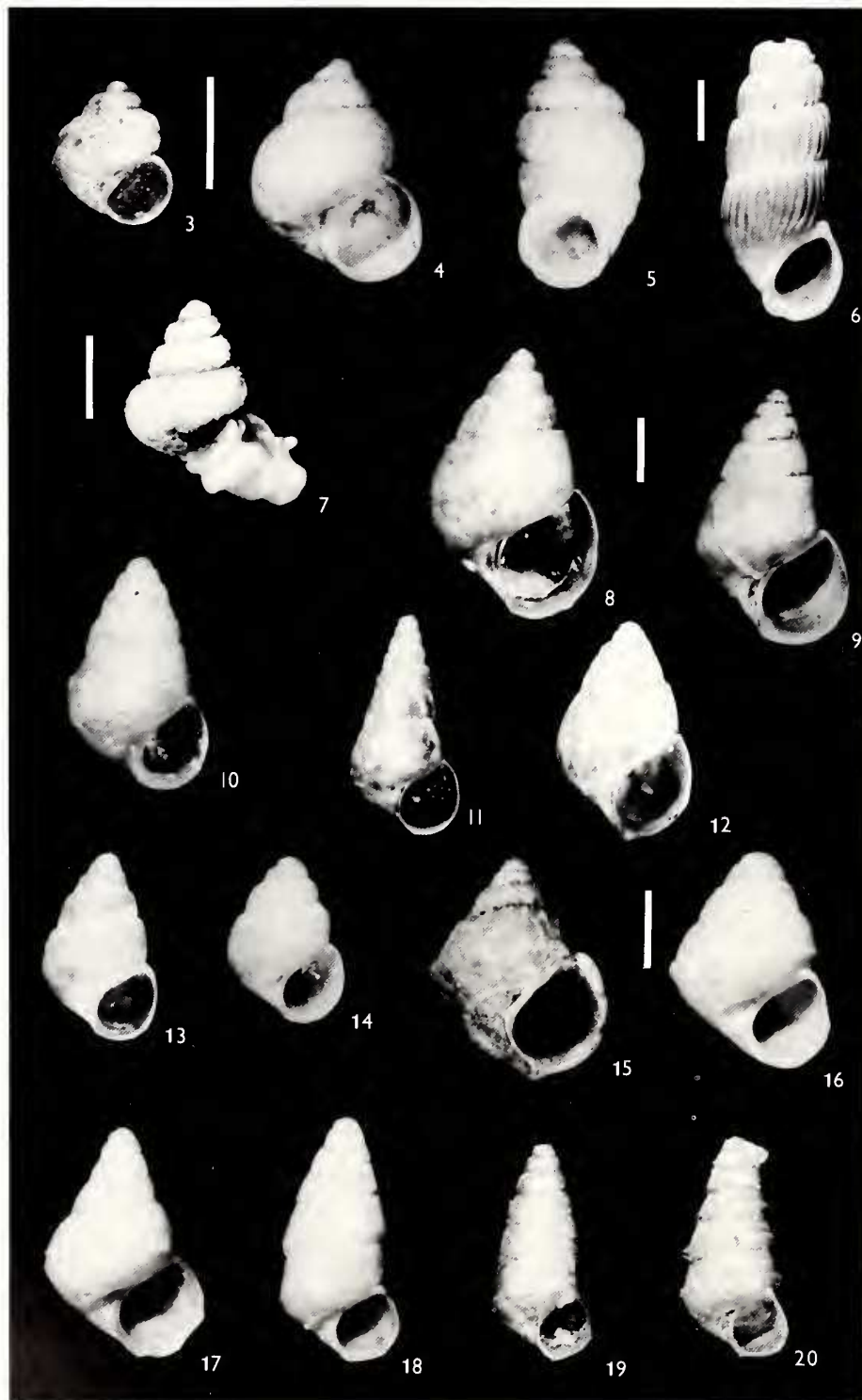
Order STYLOMMATOPHORA

Family ACHATINELLIDAE

Genus *Pacificella* Odhner, 1922*Pacificella ?variabilis* Odhner, 1922

Fig. 26

Species of *Pacificella* are widely distributed on Pacific islands and were recorded from the Mariana Islands without specific locality data (Cooke and Kondo, 1961; Preece, 1995). Its wide range indicates it could have been



Figs. 3-20. Land snails from Rota. Site numbers for each species are from Fig. 2 and are listed after the species name. 3. *Georissa elegans*, 20. 4. *G. laevigata*, 20. 5. *Palaina taeniolata*, 12. 6. Truncatellidae sp., 3. 7. ?*Allepithema* sp. 1, 6. 8. *Omphalotropis cookei*, 8. 9. *O. elongatula*, 1. 10. *O. laevigata*, 12. 11. *O. octogyra*, 26. 12. *O. semicostulata*, 20. 13. *O. cf. submaritima*, 12. 14. *O. sutralis*, 25. 15. *O. quadrasi*, 21. 16. *O. 'carina'* sp. 1, 20. 17. *O. 'carina'* sp. 2, 20. 18. *O. 'carina'* sp. 3, 20. 19. *O. 'carina'* sp. 4, 20. 20. *O. 'carina'* sp. 5, 20. Scale bars = 1 mm except Fig. 4 = 2 mm. Fig. 1 scale bar also refers to Figs. 4, 5, and 10. Fig. 6 scale bar also refers to Figs. 12-14 and 18-20. Fig. 8 scale bar also refers to Figs. 9, 11, and 15. Fig. 16 scale bar also refers to Fig. 17.

introduced aboriginally onto the Mariana Islands. Live animals were found at one site on Rota, on the undersides of tree leaves.

Genus *Lamellidea* Pilsbry, 1910

Lamellidea microstoma (Quadras and Moellendorff, 1894)

Cooke and Kondo (1961) reviewed this species. It was not encountered during the present surveys. It was figured by Zilch (1962).

Lamellidea subcylindrica (Quadras and Moellendorff, 1894)

Fig. 27

This species is known only from Guam and Rota (Cooke and Kondo, 1961). Cooke and Kondo (1961) noted this to be a less abundant species than *Lamellidea microstoma* on both Guam and Rota. The second species of *Lamellidea* known in the Marianas (*L. microstoma*) was not found on Rota in 1994 or 1995. Live animals of *L. subcylindrica* were collected from the undersides of tree leaves.

Genus *Elasmias* Pilsbry, 1910

Elasmias quadrasi (Moellendorff, 1894)

Fig. 28

This species is distinguished from other achatinellids on Rota by its small size (ca. 2.5 mm length) and distinct apertural barriers. *Elasmias quadrasi* is known from Guam, Rota, Tinian, and Saipan and extends onto the northern Mariana Islands (Cooke and Kondo, 1961). Live animals were found aestivating on the undersides of leaves and twigs in trees.

Family PUPILLIDAE

Genus *Gastrocopta* Wollaston, 1878

Gastrocopta sp(p).

Fig. 29

Gastrocopta is a wide-ranging genus that apparently was in part distributed by humans (Solem, 1959, 1988). No living specimens were found on Rota. Records at the Bishop Museum indicate a species of *Gastrocopta* was alive on Rota in 1949 (BPBM 213220, 213221).

Genus *Nesopupa* Pilsbry, 1900

Nesopupa sp(p).

Fig. 30

Australian *Nesopupa* were reviewed by Solem (1988). No live *Nesopupa* were found on Rota in 1995. *Nesopupa* (*Nesopupa quadrasi quadrasi*) (Moellendorff, 1894) was described from Guam. A few records of live

Nesopupa on Rota were found at the Bishop Museum (e.g. BPBM 82202, 82429), indicating that live specimens were collected in 1925 by H. G. Hornbostel. The wide range of many *Nesopupa* species are indicative of human transport. Specific identification of this material was not made.

Family PARTULIDAE

Genus *Partula* Férussac, 1821

Partula gibba Férussac, 1821

Fig. 31

Partula gibba is endemic to the Mariana Islands, ranging from Guam through the northern Mariana Islands (Kondo, 1970). This was a widespread species on Rota at one time attested by the large number of subfossils found at almost all sites visited and the large number of live-collected specimens housed at the Bishop Museum. Only five of the sites surveyed now support living populations of *P. gibba*, indicating that this species has declined greatly in recent years. A similar decline for *P. gibba* was documented by Hopper and Smith (1992) on Guam.

Partula cf./aff. *gibba* Férussac, 1821

Fig. 32

Four shells of a distinctive *Partula* were collected from paleontologic test pits at Payapai and As Matmos caves. They are close in general shell shape to *P. gibba*, but differ in having an extremely thickened and heavy shell. Similar shells were not mentioned in Crampton's (1925) monograph on variation in Partulidae of the Mariana Islands. Limited material leaves the status of these shells uncertain; they could represent an extinct undescribed (sub)species or local race of *P. gibba*.

Genus *Samoana* Pilsbry, 1909

Samoana fragilis (Férussac, 1821)

No shells of this species were found in 1995. Bishop Museum records indicate *Samoana fragilis* once occurred on Rota, on the Sabana in 1959 (BPBM 213164-213168). Today the Sabana area has been mostly converted into agricultural fields and no living partulids were found there in 1995. During a short field trip in 1996 to Rota, a colony of *S. fragilis* was found at site 24.

Family STREPTAXIDAE

Genus *Gonaxis* Taylor, 1877

Gonaxis kibweziensis (Smith, 1894)

This species was introduced to Rota probably from Aguijan where it was released as a possible control agent for *Achatina fulica*. Shells of this species were found at site 2. I know of no further information about this species on Rota other than it was alive in 1969 (Eldredge, 1969).



Figs. 21-40. Land snails from Rota. Site numbers for each species are from Fig. 2 and are listed after the species name. 21. *Omphalotropis* sp. 6, 6. 22. *O.* sp. 7, 25. 23. *Paludinella conica*, 24. 24. ?*Quadrasiella* sp. 1, 20. 25. *Q. clathrata*, 20. 26. *Pacificella* ?*variabilis*, 20. 27. *Lamellidea subcylindrica*, 20. 28. *Elasmias quadrasi*, 20. 29. *Gastrocopta* sp(p), 12. 30. *Nesopupa* sp(p), 1. 31. *Partula gibba*, 8. 32. *P.* cf./aff. *gibba*, 20. 33. *Succinea* sp(p), 13. 34. *Himeroconcha* sp. 1, 20. 35. *H.* sp. 2, 20. 36. *Semperdon heptptychius*, 1. 37. *S.* sp. 1, 20. 38. *Liardetia* sp(p), 1. 39. *Lamprocystis* sp(p), 1. 40. ?Genus, 20. Scale bars = 1 mm except 31, 32 = 4 mm and 33 = 3 mm. Fig. 26 scale bar also refers to Figs. 29 and 30. Fig. 22 scale bar also refers to Figs. 23, 27, 34-37, and 39. Fig. 21 scale bar also refers to Figs. 25 and 28. Fig. 24 scale bar also refers to Figs. 38 and 40.

Family SUBULINIDAE

Genus *Subulina* Beck, 1837*Subulina octona* (Bruguière, 1789)

Subulina octona, a human-transported species, was reviewed and figured by Solem (1988). On Rota it was noted alive at several sites, although I did not collect this species. It apparently is surviving well on the island. On many islands it is noted for inhabiting cultivated gardens.

Family SUCCINEIDAE

Genus *Succinea* Draparnaud, 1801*Succinea* sp(p).

Fig. 33

The number of species of *Succinea* on Rota could not be determined because they cannot be separated easily by shell characters alone (Cowie *et al.*, 1995). Four species of *Succinea* were recorded from Guam (Smith, 1993), two of which were figured by Zilch (1978). Bishop Museum records indicate *Succinea* was widespread and living on the island in 1925 and 1949 (*e.g.* BPBM 213287-213289). *Succinea* might be extirpated from Rota.

Family ACHATINIDAE

Genus *Achatina* Lamarck, 1799*Achatina fulica* Bowdich, 1822

Achatina fulica, an introduced agricultural pest, was once extremely common on Rota, demonstrated by the large numbers of shells seen at many sites (Muniappan, 1983). Several surveys were conducted during the late 1940s and early 1950s by Bishop Museum staff and associates to ascertain the status of *A. fulica* in the Mariana Islands (Lange, 1950; Mead and Kondo, 1950; Chamberlin, 1952; Kondo, 1952). The occurrence of this species was not tracked during 1994 and 1995 because its previous distribution on the island is known. No living animals or fresh shells were seen during surveys in 1994 or 1995. However, residual populations could still exist on Rota in agricultural areas, which were not surveyed during 1994 or 1995.

Family CHAROPIDAE

Solem's (1976, 1983) monographs provide the systematic framework for the Mariana Island charopids. No living specimens of any charopid were found during 1995 or 1996 surveys, although Bishop Museum records and records in Solem (1983) indicate they were once common. All Rota charopids could be extirpated. Many of the specimens collected were either fragmentary or too obscured by soil to make species identification possible (indicated on Table 2 as "charopid sp(p). indet.").

Genus *Himeroconcha* Solem, 1983*Himeroconcha* sp. 1

Fig. 34

This apparently undescribed species appears to fit

within *Himeroconcha* generic limits set by Solem (1983). It differs from *H. rotula* (Quadras and Moellendorff, 1894) by its rapidly descending body whorl. A single shell of this species was collected at each of two sites.

Himeroconcha sp. 2

Fig. 35

Eight subfossil specimens of another apparently undescribed *Himeroconcha* were found at site 12. Three complete specimens show this species to fall within the generic limits set for *Himeroconcha* by Solem (1983). The apertural periphery of *Himeroconcha* sp. 2 is expanded compared to that of *H. rotula*. The body whorl of *H. sp. 2* does not descend as rapidly as in *H. sp. 1*.

Genus *Semperdon* Solem, 1983*Semperdon heptapychius*

(Quadras and Moellendorff, 1894)

Fig. 36

Shells of this species were found at two sites on Rota. Previously the species was known only from Guam (Solem, 1983).

Semperdon rotanus Solem, 1983

Semperdon rotanus was described and thoroughly reviewed by Solem (1983). It was not encountered during the present survey.

Semperdon sp. 1

Fig. 37

Semperdon sp. 1 is easily distinguished from other Rota *Semperdon* species by its extremely high spire. It was found at one site as rare subfossils.

Family HELICARIONIDAE

Genus *Liardetia* Gude, 1913*Liardetia* sp(p).

Fig. 38

Two species of *Liardetia* were recorded from Rota by Baker (1938): *L. doliolum* (Pfeiffer, 1846) and *L. tenuisculpta* (Moellendorff, 1893). The identification of new material from my collections is uncertain at this stage. *Liardetia* specimens were collected from screw pine leaves and other vegetation by using a beating sheet. The genus seems to survive well on Rota and appears not in decline.

Genus *Lamprocystis* Pfeffer, 1883*Lamprocystis* sp(p).

Fig. 39

One species of *Lamprocystis* was recorded from Rota by Baker (1938): *L. fastigata* (Gude, 1917). The identification of new material in my collections is uncertain at

this stage. Living specimens were found on the underside of decaying leaves on the forest floor. At site 1, *Platydemus manokwari* was noted on the underside of a rotting leaf alongside four adults of *L. sp(p)*. Very few living specimens of *L. sp(p)* were found on Rota, although they were fairly abundant at site 24.

Family ?

Genus ?

Fig. 40

The taxonomic affinity of this species is uncertain at present. It resembles the many Achatinellidae in that it has an unsculptured shell, with a strong and large parietal barrier present. It was found only at the paleontological excavation at Payapai Cave.

DISCUSSION

This is the first review of the land snail fauna of Rota. I have recorded a total of at least 43 species during the 1994, 1995, and 1996 surveys. Several taxa, however, were identified only to genus and could contain multiple species. Thus among helicarionids, I identified specimens only to the genera *Liardetia* and *Lamprocystis*; Baker (1938) recorded three helicarionid species from Rota (*Liardetia tenuisculpta*, *L. doliolum*, and *Lamprocystis fastigata*). The pupillids (*Gastrocopta sp[p]*, and *Nesopupa sp[p]*.) and the truncatellid taxa were not identified to the species level in my collections. Two additional land snail species have been recorded in the literature from Rota which were not encountered in the present survey: *Lamellidea microstoma* (Achatinellidae) and *Semperdon rotanus* (Charopidae) (Cooke and Kondo, 1961; Solem, 1983).

This brings the total native and introduced fauna of Rota to at least 46 taxa, noticeably fewer than the ca. 74 species known from Guam. This difference possibly reflects in part the much lower intensity of sampling that Rota has received compared with Guam, but could also be due to the island's smaller size and greater habitat homogeneity.

Three species (*Subulina octona*, *Achatina fulica*, and *Gonaxis kibweziensis*) are certainly introductions while three others (*Nesopupa sp[p]*., *Gastrocopta sp[p]*., and *Pacificella ?variabilis*) are potential introductions (Cook and Kondo, 1961; Solem, 1988). One additional species remains unidentified even to family and is not considered further below. This leaves at least 39 taxa as indigenous to Rota.

Eighty-five percent of the indigenous species appear to be endemic to the Mariana Islands. Of the three indigenous species that are known to be more widespread,

Liardetia doliolum and *L. tenuisculpta* are recorded from the Philippines and the Caroline Islands while *Pythia scarabaeus* is widespread throughout western Pacific islands (Baker, 1938).

Thirty-six percent of the Mariana endemic taxa are known from Rota only. These are possible Rota endemics. Guam is the closest island to Rota and also has the best known modern land snail fauna of any Mariana Island. However, Guam's fossil fauna is still poorly known, and some of the species recorded as Rota endemics might have existed on Guam in the past.

Restriction of species ranges to single islands is characteristic of land snails and many insect groups (*e. g.* weevils) on central Pacific islands (Crampton, 1925; Baker, 1938; Cooke and Kondo, 1961; Paulay, 1994). As noted above, most of the Rota land snails occur on neighboring islands also (*i.e.* Guam and anecdotally from Tinian and Saipan). Within the Mariana Islands, wide multi-island species ranges have been found to be the rule among the systematically revised families Achatinellidae, Partulidae, and Helicarionidae (Baker, 1940; Cooke and Kondo, 1961; Kondo, 1970). The other taxonomically well-known family, the Charopidae, has not been extensively collected on the Mariana Islands outside of Guam. For other historically recorded non-introduced families (Hydrocenidae, Diplommatinidae, Truncatellidae, Assimineidae, Ellobiidae, and Succineidae) little is known about the ranges of component species among the southern Mariana Islands. Observing that many land snail species are widely distributed among the Mariana Islands implies the existence of an effective dispersal mechanism.

To evaluate whether the proportion of single island endemics is indeed relatively low in the Mariana Islands compared with other Pacific islands, I compared the proportion of single island endemics on Rota and on Oahu (Hawaiian Islands). The fauna of the Hawaiian Islands was chosen for comparison, because it is taxonomically well known at the entire faunal level (Cowie *et al.*, 1995; Cowie, 1996). Oahu was chosen as a representative island from that archipelago.

A much larger proportion of Oahu's (87%, N = 283) than of Rota's (31%, N = 39) indigenous land snail fauna is constituted by single island endemics ($G = 54.5$; $p \ll 0.001$). The greater proportion of widespread species in the Marianas than in the Hawaiian Islands could be the result of several factors. A larger proportion of Rota's fauna is comprised of prosobranchs, which might be better dispersers by virtue of the protection provided by their operculum. Thus while 59% of the indigenous land snails of Rota are prosobranchs, only 2% of the Oahu land snails are. However, the remaining pulmonates are still significantly ($G = 30.5$; $p \ll 0.001$) more often single island endemics on Oahu (87%, N = 278) than on Rota (25%, N = 16).

Further, all but three of the Rota pulmonate families (*i. e.*, Achatinellidae, Succineidae, Endodontoidea, and Helicarionidae) belong to groups that are well represented on Oahu. Thus it appears that phylogenetic bias is not the cause of the differences. Intra-island speciation, which generates large numbers of endemics *in situ* has progressed to large radiations in several lineages on Oahu, but less so on Rota (but see below), and this process is expected to increase endemism on Oahu. Finally the Mariana Islands lie in the western Pacific typhoon trough and are frequently battered by these catastrophic storms. Wind dispersal and transport by birds and possibly bats are believed to be perhaps the most important agents of dispersal among Pacific island land snails (Rees, 1965; Kondo, 1970; Vagvolgyi, 1975). The much greater availability of wind transport provides a site-specific explanation, and also matches observations in the marine environment, where storms have been shown to exert a major control on the distribution of marine organisms in the area (Kerr *et al.*, 1993; Kerr, 1994).

Assimineids are the most diverse family of land snails on both Guam and Rota. The Mariana Islands are the only oceanic Pacific island group with a diverse assemblage of assimineids. The Philippine Islands also support a diverse assemblage of assimineids but are continental islands. Of the 19 assimineid species recognized on Rota at this time; nine may be endemic, although six of the possible endemics are known from fewer than 20 specimens at three sites, making their identification and range among the islands tentative.

It appears that speciation within the Mariana Islands has occurred at least in the families Assimineidae, Charopidae, and Partulidae. There is clear evidence for both inter- and intra-island speciation within the Assimineidae and Charopidae. The *Omphalotropis* "carinate" species group forms a well-defined portion of the Rota assimineid fauna, with no apparent close relatives known from any of the other Mariana Islands. A single ancestral colonist is hypothesized for the radiation of the five nominal species in this complex. The frequent multi-island ranges of species in the families Assimineidae and Partulidae indicate that inter-island speciation could have been the main form of diversification in their evolutionary history. This is true as well for the Charopidae among the Mariana Islands, even though endodontoid land snails are renowned for their almost strict single-island endemism (Solem, 1983).

Habitat destruction and introduced predators appear to have caused the decline and even possible extirpation of all species in three families of pulmonate land snails (Charopidae, Succineidae, and Pupillidae) on Rota since 1949. *Pythia scarabaeus*, a member of the Ellobiidae, could also be extirpated. In addition to the invertebrate

predators, introduced feral mammals (pigs and rats) could have contributed to the decline of some species. The species in two other pulmonate families (Partulidae, Achatinellidae) have drastically declined since 1949. Partulids were abundant enough on Rota in 1969 for Eldredge (1969: 27) to state "these [partulids] are common enough to be collected for ornamentation and jewelry." In contrast, only five *Partula* populations are known to remain on Rota today.

Thirty-five of the 46 taxa known from Rota were encountered in the material from paleontological excavations at As Matmos and Payapai caves. These fossil assemblages thus represent a remarkably complete record of the island's malacofauna. The absence of many species in the material collected from the caves is readily explained: *Subulina octona*, *Achatina fulica*, and *Gonaxis kibwziensis* were introduced to the island in historic times; *Samoana fragilis* was only known from a single site on the island and has a thin fragile shell; the other four species are assimineids of which some seem to have naturally small ranges on Rota (*Omphalotropis octhogyra*, *O. quadrasi*) or are restricted to certain habitats (*O. cf. submaritima*, *O. sp. 7*). The number of land snail species recorded from these cave sites is high compared to other studies on land snail remains in archaeological settings (Christensen and Kirch, 1981; Chambers and Steadman, 1986). Paleontological excavations at As Matmos and Payapai caves reveal 13 taxa which no longer occur on the island, 11 of which cannot be matched to any species recorded previously from Guam or Rota. An abundance of *Lamellidea* shells in the paleontological excavations indicates they were much more common in the past at these two sites than they are today.

Of the 43 taxa found on Rota during 1994, 1995, and 1996 only 9% are considered surviving well, while 23% are surviving with questionable status. All families of land snails except Diplommatinidae have component species which are declining. Twelve percent of the species are potentially extirpated, while 56% of the fauna is considered to have declined. In conclusion, all evidence gathered to date suggests declines in populations, ranges, and species numbers of many land snails on Rota.

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